

Varicorbula (Bivalvia: Corbulidae) of the Western Atlantic: Taxonomy, Anatomy, Life Habits, and Distribution

PAULA M. MIKKELSEN

Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, New York, New York 10024-5192, USA; mikkel@amnh.org

AND

RÜDIGER BIELER

Department of Zoology, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, Illinois 60605-2496, USA; bieler@fieldmuseum.org

Abstract. The taxonomy, anatomy, life habits, and distribution of the three western Atlantic species of *Varicorbula* are discussed. *Varicorbula disparilis* (d'Orbigny, 1842) is recognized as valid and widely distributed, based on museum material (including lectotype designation), literature, and new collections (by Shipek grab and otter trawl) from the westernmost Florida Keys. *Corbula* [or *Notocorbula*] *operculata* Philippi, 1848, the most often applied name to this form, is considered a *nomen dubium* in the absence of locatable type material; *C. limatula* (Conrad, 1846) is confirmed as a synonym by examination of type specimens. Anatomy is largely congruent with that previously reported for members of *Varicorbula* and *Corbula*. The known geographic range of *V. disparilis* includes North and South Carolina, Georgia, eastern Florida, through the Gulf of Mexico, the Bahamas, and Yucatan, with unverified records from Virginia and several West Indian islands; it is associated with sand or mud habitats from relatively shallow depths to below 1400 m. Attached epifaunal mollusks associated with the Florida Keys samples suggest that this species lives epibenthically in densities of nearly 400 individuals/m². Two other Recent western Atlantic members of *Varicorbula* are recognized as valid, both of which had been previously synonymized by various authors with *V. disparilis/limatula/operculata*. Provisionally maintained as distinct species based on shell characters are: *C. krebsiana* C. B. Adams, 1852 (Jamaica and Puerto Rico only), and *C. philippii* E. A. Smith, 1885 (Bermuda, North Carolina, Florida, Texas, Yucatan, the Caribbean, and Brazil). A revised diagnosis of the genus *Varicorbula* is presented, based on the type species, *V. gibba* (Olivi, 1792), and new data for the species studied here. In the context of existing taxonomic definitions, *Varicorbula* is properly placed in the subfamily Caestocorbulinae (rather than Corbulinae or Caryocorbulinae), a subfamily otherwise known only from the Cretaceous and Eocene.

“Recent specimens of *Varicorbula* of the western Atlantic represent a taxonomic quandary. . .”

—L. C. Anderson, 1996: 21.

INTRODUCTION

Varicorbula disparilis (d'Orbigny, 1842) [as *Corbula*] was originally described from Guadeloupe. This species has been most frequently called *V.* [or *Corbula* or *Notocorbula*] *operculata* (Philippi, 1848), described from the Caribbean island of St. Thomas. Earlier literature finds it cited as *C. limatula* Conrad, 1846, described from the Gulf of Mexico off the western coast of Florida. Although it is often listed from offshore dredge samples (Bush, 1885a, b; Dall, 1889; Abbott, 1954, 1974; Warmke & Abbott, 1961; Weber, 1961; Odé, 1971, 1976; Waller, 1973; Porter, 1974; Porter & Wolfe, 1971; Treece, 1979; Calnan & Littleton, 1985a, b; Jensen & Harasewych, 1986; Vittor, 1998), it is usually collected only as empty

shells (Abbott, 1954, 1974; Merrill et al., 1978; Calnan & Littleton, 1985a, b; Lyons, 1989, personal observation) and nothing is known of its anatomy or biology.

During a research cruise to the Marquesas Keys and Dry Tortugas in the western Florida Keys, fortuitous and abundant living collections of this rarely live-collected myoidean clam were obtained by Shipek grab and otter trawl. This provided an opportunity to study its morphology, to make comparisons with the few existing non-conchological data recorded for the family (Yonge, 1946; Morton, 1990), to evaluate other western Atlantic species, and to re-examine distinguishing characters of this genus. In addition, the samples allowed unique observations on population structure and life habits.

MATERIALS AND METHODS

This study is part of an ongoing investigation of marine molluscan biodiversity in the Florida Keys (Bieler &

Table 1
R/V *BELLOWS* stations in which *Varicorbula disparilis* specimens were collected.

Sta. no.	Date (1997)	Location	Coordinates	Depth (m)	Gear
FK-075	22 April	NNW or Marquesas Keys; mud	24°44'05"N, 82°14'24"W	21	Shipek grab
FK-077	22 April	NNW of Marquesas Keys	24°45'00"N, 82°15'00"W	21	Shipek grab
FK-078	22 April	due E of New Ground, NW of Marquesas Keys	24°40'40"N, 82°16'46"W	12	Shipek grab
FK-082	22 April	NNW of New Ground, between Marquesas Keys and Dry Tortugas	24°48'17"N, 82°28'42"W	27	Shipek grab
FK-084	22 April	N of Rebecca Shoal, between Marquesas Keys and Dry Tortugas	24°44'24"N, 82°37'24"W	29	Shipek grab
FK-085	22 April	NNW of East Key, Dry Tortugas; thick clay	24°49'12"N, 82°43'54"W	33	Shipek grab
FK-096	24 April	due S of Dry Tortugas	24°19'48"N, 82°54'06"W	223	Shipek grab
FK-098	24 April	due S of Dry Tortugas	24°24'48"N, 82°52'36"W	60	Shipek grab
FK-100	25 April	S of East Key, Dry Tortugas	24°34'18"N, 82°46'54"W	31	Shipek grab
FK-104	25 April	NNE of New Ground, between Marquesas Keys and Dry Tortugas	24°47'18"N, 82°18'18"W	23	Shipek grab
FK-106	25 April	NNE of New Ground, between Marquesas Keys and Dry Tortugas	24°47'18"N, 82°18'18"W to 24°48'12"N, 82°19'06"W	23–24	25' otter trawl (~1 hr bottom time)

Mikkelsen, 1999), formally initiated by the authors in 1994. Samples were collected during a four-day research cruise to the Dry Tortugas, the westernmost Florida Keys, aboard R/V *BELLOWS* (Florida Institute of Oceanography, St. Petersburg, Florida). Thirty-five living specimens of *Varicorbula disparilis* were obtained in one Shipek grab sample (sta. FK-104, see Table 1 for locality data for all cited stations). An immediately subsequent otter trawl sample (sta. FK-106) brought aboard another estimated 3200 specimens entangled within an elastic, grey fibrous mat covering the trawl's "tickle chain" (Figures 1, 2).

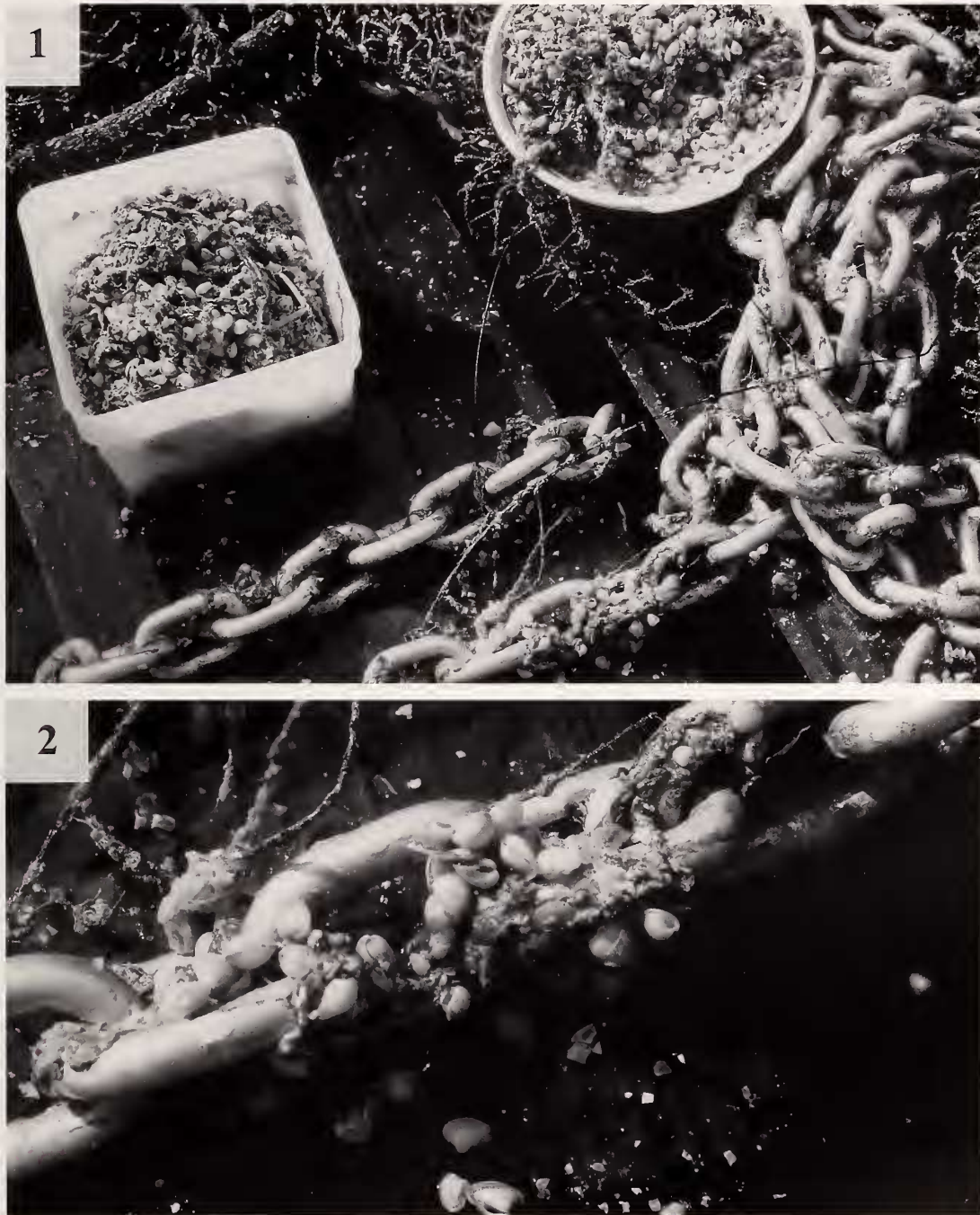
Living clams were hand separated from the Shipek grab sample, relaxed in aqueous magnesium sulfate, and fixed in 5% formalin (later transferred to 70% ethanol); the remainder was sieved through a 350 μ m sieve to remove fine sediment, then dried. The trawl sample included the fibrous mat with the living clams; both were manually removed from the chain. While still aboard ship, the clams were hand separated from the mat, relaxed, fixed, and preserved as above; the mat fragments were preserved in 70% ethanol. Empty shells of *Varicorbula disparilis* were collected in other Shipek grab samples in the same general vicinity in the Gulf of Mexico (stas. FK-075 through 100).

For histological examination, shells were removed manually from formalin-fixed, ethanol-preserved specimens (sta. FK-106). The specimens were dehydrated through a graded ethanol series, followed by clearing in xylene substitute (Hemo-De®, Fischer Scientific, Pittsburgh, Pennsylvania), and embedding in paraffin (Paraplast X-tra®; Oxford Labware, St. Louis, Missouri). Complete 7- μ m serial sections were produced for intact individuals in lateral or anteroposterior orientation, and

stained with hemotoxylin/eosin. Histological sections and dried shells were photographed under light microscopy. For scanning electron microscopy, dried shells and critical-point dried animals were mounted on stubs, coated with gold-palladium, and scanned on a Zeiss DSM-950 scanning electron microscope at AMNH.

Synonymies herein are restricted to original descriptions, significant taxonomic works, and descriptions and geographical records verifiable through published illustrations or museum lots. Cited repositories are: AMNH, American Museum of Natural History (New York); ANSP, Academy of Natural Sciences of Philadelphia; BMNH, The Natural History Museum (London); DMNH, Delaware Museum of Natural History (Wilmington); FMNH, Field Museum of Natural History (Chicago); HMNS, Houston Museum of Natural Science (Texas); MCZ, Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts); NCSM/IMS, North Carolina State Museum of Natural Sciences (Raleigh); SBMNH, Santa Barbara Museum of Natural History (California); UMMZ, University of Michigan, Museum of Zoology (Ann Arbor); USNM, National Museum of Natural History, Smithsonian Institution (Washington, D.C.).

Selected material examined: *Varicorbula disparilis* (d'Orbigny, 1842) (39 lots, 3088+ specimens): NORTH CAROLINA: SE of Cape Lookout, 34°24.3'N, 76°35.9'W, grab, 24 m. Duke University BLM Project #65818252, 13 August 1981, NCSM/IMS 9276 (6 alc.); R/V *OREGON* #6516, SE of New River Inlet, 34°17' to 34°16'N, 77°11' to 77°14'W, 13 fms (24 m), Porter!, 24–25 March 1967, NCSM-IMS 3008 (20+, some live collected). SOUTH CAROLINA: R/V *EASTWARD* sta. #11545, off Charleston, 32°41.8'N, 78°32.4'W, coarse sand, 50 m, H. J. Porter!, 16 March 1969, NCSM/IMS 2868 (20+) (Porter, 1975).



Figures 1, 2. *Varicorbula disparilis* entangled in byssal mat, as captured on the tickle chain of an otter trawl.

GEORGIA: R/V *DAN MOORE*, ESE of Savannah, Calico Scallop Grounds, 31°54'N, 79°49'W, modified tumbler dredge, 20–22 fms (37–40 m), sand, 22 January 1978, NCSM/IMS 7459 (1 alc., 53 dry). EASTERN FLORIDA: R/V *GOSNOLD* Cr. 222, sta. 273a, off Ft. Pierce, 27°34.0'N, 80°02.2'W, pipe dredge, 37 m, D. K. Young!, 28 February 1974, HBOM 064:01469 (7 + 260 valves, in alcohol); 10 nmi (18.5 km) off Ft. Pierce, St. Lucie County, 27°33.25'N, 80°03.2'W, dredged, 33 m, R. W. Virnstein!,

November 1977, DMNH 179615 (50+); R/V *JOHNSON* Cr. 045, Re-col. sta. II, 25.4 km east of Ft. Pierce, St. Lucie County, 27°33.2'N, 80°03.2'W, recolonization tray experiment (uncovered compartment), 33 m, R. W. Virnstein!, 14 August 1977, HBOM 064:01908 (53, in alcohol); off Palm Beach, 50 fms (91.5 m), T. L. McGinty!, June 1940, FMNH 23497 (3); off Palm Beach County, 3 fms (5.5 m), Donovan!, July 1940, AMNH 232601 (4); Gulf Stream, out from Bounton [*err pro* Boynton Beach?],

Palm Beach County, 35–45 fms (64–82 m), F. Lyman!, 1940, FMNH 20352 (5); 7 ms south from Fowey Rocks Light, Dr. W. H. Rush!, ANSP 50908 (5 valves). FLORIDA KEYS: shell shop purchase, dredged, 50 m, E. S. Phillips Collection, SBMNH 55425 (5); off Alligator Reef Light, 600 ft (183 m), J. Moore! 1965, ANSP 312497 (20+ valves); north of Key West, 80–150 ft (24–46 m), September 1963, AMNH 144874 (1); Dry Tortugas, 60–45 fms, Dr. W. R. Taylor!, 1925, ANSP 141066 (17 valves). WESTERN FLORIDA (GULF OF MEXICO): Gulf of Mexico, Smith!, 1962, FMNH 151867 (2); Gulf of Mexico, J. Moore!, FMNH 223517 (ex FMNH 165115) (1); Gulf of Mexico, off Florida, deep water, ANSP 50909 (lectotype + 2 paralectotypes; see text); west of Boca Grande, dredged, 170 ft (52 m), coral rubble and clay, J. Moore!, AMNH 182093 (2); southwest of Anna Maria Island, dredged, 300–400 ft (91–122 m), J. Moore!, AMNH 107795 (1); southwest of Egmont Key, N. Hepler!, 1971, DMNH 45248 (5); west of Egmont Key, 300 ft (91 m), J. Moore!, July 1964, ex Germer Collection, AMNH 273277 (14); southwest of John's Pass [St. Petersburg], 27 fms (49 m), Steger! 1965, ANSP 306297 (in part) (11); west of Anclote Key, 90–100 ft (27–30.5 m), J. Moore!, December 1967, AMNH 180242 (2); west of Bayport, 150 ft (46 m), J. Moore!, May 1963, ex Germer Collection, AMNH 273274 (13); 90 mi (145 km) west of Crystal River, dredged, 30 fms (55 m), J. Moore!, 1963, ex Feinberg Collection, AMNH 176008 (3); west of Cape San Blas, east edge of DeSoto Canyon, 100–300 fms (183–549 m), D. & R. Black!, 1971, AMNH 167213 (8); off Cape San Blas, 29°33.5'N, 84°38'W, 10 fms (18 m), H. Kritzler!, 22 January 1972, DMNH 50261 (5); off Panama City, 30°01.0'N, 86°20.0'W, M. Jones!, 08 April 1958, AMNH 145190 (1); off Destin, 14 fms (26 m), T. L. McGinty!, ANSP 25214 (50+ valves); off Destin, dredged, 15 fms (27.5 m), September 1940, ex Wisoff Collection, AMNH 120491 (6 + 1 valve). GULF OF MEXICO (OTHER STATES): Alabama, south of Mobile, 30°04'30"N, 88°36'W, 62–68 ft (19–21 m), D. R. Moore! 27 June 1960, ex Odé Collection, HMNS 14992 (5); Louisiana, 120 mi southwest of Marsh Island, D. Moore!, ANSP 209696 (12 valves); Louisiana, 98.5 mi SSE of Cameron, Three Hickey Rock, 28°20'45"N, 92°26'30"W, shale dome, Northwest Gulf Survey Collection Sta. 1679 (lot 20352), diver, 50–60 ft (15–18 m), 07 July 1972, HMNS 7437 (3 valves); Louisiana, mouth of Mississippi River, mudlumps at South Pass, Northwest Gulf Survey Collection Sta. 1684 (lot 19515), surface collected, E. & H. Vokes!, HMNS 7363 (500+ valves); Texas, 74 mi SSE of Galveston, Stetson Bank, dredged, 10–50 fms (18–91 m), Northwest Gulf Survey Collection Sta. G3Sh17 (lot 7380), T. E. Pulley & P. McGee! 1963, HMNS 7345 (1650 valves); Texas, 32.5 mi N of Port Isabel, 26°36'N, 97°08'W, trawl, 12 fms (22 m), Northwest Gulf Survey Collection Sta. G32W61 (lot 5101), GUS III, 10–25 August 1965, HMNS 7347 (9 + 249 valves). BAHAMAS: New Providence Island, Nassau Harbor, dredged, AMNH 80773 (1 + 4 valves); Andros, Fresh Creek, off Coakley Town, 400 fms (732 m), MOTHER GOOSE II, J. Armstrong!, June 1950, AMNH 134068 (1 valve); Bimini Island, 03 September 1947, AMNH 91429 (1 valve).

Vouchers for this study: FK-104 (AMNH 290090, 35 specimens); FK-106 (AMNH 290087, 500; DMNH 209190, 100; FMNH 278463, 100; UMMZ 255298, 10+).

Varicorbula krebsiana (C. B. Adams, 1852) (9 lots, 100 specimens): JAMAICA: DMNH 21941 (1 paralectotype, ex ANSP 297148 [2 paralectotypes, *vidi*]); C. B. Adams!, ANSP 297148

(2); ex Haines Collection, AMNH 33808 (1); ex Swift Collection, ANSP 50899 (3); Kingston Harbor, between Kingston and Port Royal, 3–4 fms (5.5–7 m), [muddy bottom, *fide* C. B. Adams, 1852: 234], C. B. Adams! [Acc. 1173, ex C. B. Adams Colln., ex. Amherst College, 1942] MCZ 155611 (1 lectotype, with note "spec. fig'd by Dall" [1886: pl. 1, figs. 1. la, b]); same data, MCZ 155612 (paralectotypes: 10 + 26 each separated right and left valves, 2 fragments); same data, ex MCZ ex Adams Collection, ANSP 182624 (paralectotypes, 4 + 1 valve). PUERTO RICO: Montalva Bay, Enunado, J. Poling!, AMNH 85095 (21 + 4 valves), FMNH 278465 (12, ex AMNH 85095); Laurel Reef, off La Parguera, dredge, 75 ft (23 m), G. L. Warmke! 15 June 1956, ANSP 222748 (5 + 6 valves).

Varicorbula philippii (E. A. Smith, 1885) (37 lots, 402+ specimens). BERMUDA: 1.5 mi (2.4 km) south of Castle Roads channel, J. Lightbourn!, 13 September 1975, DMNH 106570 (2); 1.5 mi (2.4 km) south of Castle Roads channel, dredged 40–60 fms (73–110 m), J. Lightbourn!, 13 September 1975, ex R. Jensen Collection, DMNH 202580 (1 valve). NORTH CAROLINA: R/V EASTWARD sta. 10496, 34°09.5' to 34°10'N, 76°09.7'W, 50 m, Day dredge, Porter & Jenner!, 08 October 1968, NCSM/IMS P-4693 (1); R/V DAN MOORE sta. #0365, SSE of Cape Hatteras, 35°00'N, 75°28'W, scallop dredge, 26 fms (47 m), H. J. Porter!, 01 October 1968, NCSM/IMS 3186 (58, incl. 2 live collected). EASTERN FLORIDA: R/V JOHNSON Cr. 005, JOHNSON-SEA-LINK-I dive #274, 27°10.7'N, 80°02.7'W, off St. Lucie Inlet, Martin County, 22.9 m, T. Askew! (lockout diver), 25 July 1975, HBOM 064:01118 (2); R/V GOSNOLD Cr. 222, Sta. 267b, 27°08.2–08.0'N, 080°00.0–079°59.7'W, 62 m, Smith-McIntyre grab, D. K. Young!, 26 February 1974, HBOM 064:00657 (1); off Palm Beach County, 30 fms (5.5 m), Donovan!, July 1940, AMNH 128166 (20); off Palm Beach County, 3 fms (55 m), Donovan!, July 1946, AMNH 129433 (2); off Palm Beach, dredged, T. L. McGinty!, June 1940, ANSP 178586 (4) and DMNH 21944 (1, ex ANSP 178586); off Palm Beach, dredge, 300 fms (549 m), ex Bales Collection no. 12452, ANSP 221298 (4); off Palm Beach Inlet, dredged, 50 fms (91.5 m), July 1940, AMNH 144099 (21 + 3 valves); Lake Worth, Boynton [Beach], T. McGinty! June 1938, ANSP 174911 (1); east of Government Cut, Miami, 27 fms (49 m), rocky, T. L. Moise!, 30 April 1954, ANSP 194291 (6). WESTERN FLORIDA (GULF OF MEXICO): Gulf of Mexico, J. Moore!, FMNH 165115 (4); Pelican Shoal [Lower Florida Keys], J. B. Schwengel!, 1940, FMNH 77960 (16 valves); off Dry Tortugas, 280 ft (85 m), dredge, J. Moore! October 1969, ex Sartor Collection, HMNS 35531 (1); southwest of John's Pass, 27 fms (49 m), Steger! 1965, ANSP 306297 (in part) (4); southwest of John's Pass, D. Steger!, DMNH 21943 (ex ANSP 306297) (1); south-southwest of John's Pass, 34 fms (62 m), D. Steger!, 1977, DMNH 124336 (8) and DMNH 124339 (50+); south-southwest of John's Pass, 29 fms (53 m), D. Steger!, 1977, DMNH 124326 (3) and DMNH 124343 (3); south-southwest of John's Pass, 27 fms (49 m), D. Steger!, 1977, DMNH 124332 (50+); southwest of Anna Maria Island, dredged, 300–400 ft (91–122 m), J. Moore!, AMNH 232603 (4) and HMNS 962 (in part) (1); west of Anna Maria Island, dredged, 400 ft (122 m), J. Moore!, Summer 1964, ex Bijur Collection, AMNH 248383 (21 + 27 valves); off Egmont Key, dredged, J. Moore!, 170 ft (52 m), April 1996, ex Hicks Collection, AMNH 248935 (10 + 10 valves); west of Egmont Key, 300 ft (91 m), J. Moore!, July 1964, ex Germer Collection, AMNH 232604 (2). TEXAS (GULF OF MEXICO): Stetson Bank, 74 mi SSE of

Galveston, dredged, 10–50 fms (18–91 m), Northwest Gulf Survey Collection Sta. G3Sh17 (lot 7380), T. E. Pulley & P. McGee! 1963, HMNS 7345 (in part) (5 + 9 valves). ANTILLES: Grand Cayman, George Town Harbor, by the stack, A. J. Ostheimer III! sta. D-15, ANSP 209868 (1); Dominican Republic, Pt. Trujillo, outside Yuncu Reef, 15–25 fms (27.5–46 m), D. Pease!, 1933, AMNH 94671 (7 + 13 valves); same as previous, D. Pease!, 1932, AMNH 94733 (7 + 11 valves); Virgin Islands, St. John, ex Stamford Museum, DMNH 185976 (1); Grenada, West Grenada, Grand Mal Bay, “Fontenoy,” 36–48 ft (11–15 m), shell/sand/grass, R. Ostheimer! 12 February 1964, ANSP 297010 (1); Tobago, Scarborough, 2 mi south of Fort George, 36 fms (66 m), R. W. Foster! 20 April 1950, ANSP 246146 (2 valves). CENTRAL AMERICA: British Honduras [Belize], west of Blue Ground Range, Main Channel, 16°48'10"N, 88°09'20"W, sta. 72, soft mud, 79 ft (24 m), R. Robertson!, 15 August 1961, ANSP 283001 (3).

For comparative purposes:

Varicorbula gibba (Olivi, 1792): Heligoland Island, Germany, W. Mansen!, AMNH 92367 (20+ valves); Lubworth Bank, Dorset, English Channel, A. Brokershire!, Lanning Coll., AMNH 275995 (6) and AMNH 275996 (5); Dublin Bay, Ireland, Germer Coll., AMNH 260456 (10 valves); La Val André, Bretagne, France, April 1966, AMNH 178089 (2); Patras, Greece, Nelson Coll., FMNH 158519 (6 + 1 valve).

Notocorbula vicaria Iredale, 1930: Australia, Haines Coll., AMNH 33845 (6).

RESULTS

Varicorbula Grant & Gale, 1931

Varicorbula Grant & Gale, 1931:12, footnote to p. 420.—Vokes, 1945:12, 13.—Keen, 1969:N695.—Anderson, 1996:20.

For list of previously accepted synonyms, see Vokes, 1945:12.

Type species: *Tellina gibba* Olivi, 1792, by original designation; western Europe and the Mediterranean Sea (and introduced to Australia; Lamprell et al., 1998).

Diagnosis: Shell trigonal, rather thin but sturdy, bluntly truncated posteriorly, strongly inequivalve; left valve smaller, flatter, less rostrate; right valve larger, more inflated. Both valves concentrically sculptured, but discrepantly so; right valve with coarser, higher ridges; left valve with finer concentric ridges, crossed by radial ridges. Umbones prosogyrous, higher and more inflated in right valve, without nepionic caps. Periostracum on the left valve forming overlapping foliations and radial lines, overhanging shell edge substantially. Right valve with large knob-shaped tooth, articulating with deep socket in left valve. Elongated plate (“left cardinal tooth” of Yonge, 1946:fig. 2) posterior to socket of left valve, including resilium-bearing chondrophore; complimentary right chondrophore on shell within embayment posterior to tooth. Resilium oriented dorsoventrally; external ligament very small. Lateral teeth absent. Interior shell margins smooth. Deep interior groove running parallel to ventral edge of right valve, and continuing into lateral lamellae

on either side of hinge, into which margin of left valve inserts. Anterior muscle scar moderately large and crescent-shaped; posterior muscle scar oval and slightly larger. Pallial line entire (but interrupted by small gaps); pallial sinus shallow but distinct.

Remarks: No recent morphology-based phylogenetic hypothesis has yet been attempted for this family, nor are there sufficient data (conchological and/or non-conchological) to attempt one at this point. The last taxonomic revision of Corbulidae, based entirely on shell characters, was by Vokes (1945), who recognized 21 genus-group names as valid. *Varicorbula* Grant & Gale, 1931, is the appropriate genus for the present material following the diagnoses of Vokes (1945), Keen (1969), and Anderson (1996). The present material also agrees in currently accepted genus-level characters with Recent European specimens identified as *V. gibba* in the AMNH and FMNH collections and with the descriptions of the latter species by Bucquoy et al. (1896) and Yonge (1946). Although some subsequent authors (Vaught, 1989; Anderson, 1996) have adopted use of a large genus *Corbula* containing numerous conchologically defined subgenera, we treat *Varicorbula* as a full genus, in the absence of compelling reasons to support subtaxonomic categories, following Vokes (1945) and Lamprell et al. (1998).

Varicorbula is one of three recognized corbulid genera with strongly inequivalve shells (the other two being *Corbula* and *Notocorbula*); all are posteriorly rostrate and concentrically sculptured. According to Vokes (1945), *Varicorbula* is distinguished from the other two by discrepant sculpture on right and left valves, a non-rostrate smaller left valve, lacking lateral hinge teeth and a nepionic cap (= nepioconch; “resting stages” of Stenzel et al., 1957; “juvenile shell” of Iredale, 1930; characteristic of *Notocorbula*, *vide* Vokes, 1945) on the valves (which in other genera indicates subequal valves in the juvenile), and in being strongly inequivalved even as juveniles. Species of *Varicorbula* also have radial ridges (enhanced by periostracum called “epidermis” in the older literature; ridges also detectable on fossil shells) on the smaller left valve [e.g., *gibba*: Sowerby, 1820–1824:pl. 49, no. 1; Reeve, 1843:pl. 2, figs. 10a, b; Vokes, 1945:pl. 1, fig. 15; Tebble, 1966:fig. 91b; Keen, 1969:pl. E156, fig. 8d; Nordsieck, 1969:149, pl. 21, fig. 84.00; Rolán Mosquera et al., 1990:fig. 172; AMNH 275995, *vidi*; *caloosae* Dall, 1898:853 [text only]; Olsson & Harbison, 1953:pl. 13, fig. 10a; *chipolana* Gardner, 1928:pl. 34, fig. 17; *chowwanensis* Bailey, 1977:fig. 1b; *islatrinitatis* Maury, 1925:253, pl. 19, fig. 10 (also Jung, 1969:pl. 40, figs. 1, 2; Woodring, 1982:pl. 120, fig. 1); *limaula*: Vokes & Vokes, 1984:pl. 47, fig. 7c; *philippii*: Vokes & Vokes, 1984:pl. 47, figs. 7a; Figure 27; *puntacordensis* Weisbord, 1964:pl. 57, fig. 15; *sanctidominici* Maury, 1925 (Anderson, 1996:pl. 3, fig. 16); *waltonensis* Gardner, 1928:pl. 34, fig. 21]. Abbott (1974) and Lamprell et al. (1998) considered

this last feature characteristic of the genus *Varicorbula*, although radial ridges are also known in some members of Caestocorbulinae (see Discussion).

Although not noted by Lamprell et al. (1998), radial ridges are also present on the left valve in species of *Notocorbula* Iredale, 1930 [*N. vicaria* (type species; + *unicata* Hinds, 1843) Iredale, 1930:pl. 65, fig. 4; Keen, 1969:pl. E156, fig. 1b; AMNH 33845; *N. hydropica* Iredale, 1930:pl. 65, fig. 6; *N. texana* (Gabb, 1860): Stenzel et al., 1957: pl. 21, figs. 3, 5]. *Notocorbula* has been previously considered the senior synonym of *Varicorbula* (*teste* Stenzel et al., 1957; followed by Warmke & Abbott, 1961; Weisbord, 1964; Jung, 1969), based on the presence of "subdued" nepionic caps in the type species of *Varicorbula*, *V. gibba*. This explains the use of *Notocorbula* for *V. disparilis/linatula/operculata* by some authors (Warmke & Abbott, 1961; Odé, 1965, 1971; Bock & Moore, 1968; Odé & Spears, 1970; McGinty & Nelson, 1972; Morris, 1973; Porter, 1974, 1975; Rios, 1970). *Varicorbula gibba* indeed sometimes has irregular growth stoppages that could be interpreted as nepionic caps, but the presence of these is inconsistent, they are sometimes evident only on the larger right valve, and they are identically sculptured with the remainder of the valve (AMNH 92367, 275995, 260456). They are almost completely absent in the present Florida Keys material. In *Notocorbula*, the cap is invariably present in both valves and is more weakly (if not differently) sculptured from the rest of the valve (Iredale, 1930:404, 405; Vokes, 1945:pl. 1, figs. 6–10; Stenzel et al., 1957:pl. 21, figs. 2, 3, 5, 8; Keen, 1969:pl. E156, figs. 1a–c; AMNH 33845). There are many conchological similarities between *Notocorbula* and *Varicorbula*: similar hinge structure, nearly identical pallial lines and sinuses, and a smaller left valve with weaker concentric sculpture, radial sculpture, and heavier periostracum than in the right valve. The nepionic cap, when present, varies in size within a species in both genera. The keeled cardinal tooth in the right valve of *Notocorbula* (considered diagnostic by Iredale, 1930, and Vokes, 1945) does not demonstrably differ from that in *Varicorbula*, and members of both genera have a "peculiarly bipartite chondrophore" (Vokes, 1945:14, for *Notocorbula*; also Keen, 1969) also apparently present in other genera (e.g., *Caryocorbula*, *fide* Vokes, 1945; *Vokesula* Stenzel & Twining, in Stenzel et al., 1957). Nevertheless, *Varicorbula* species are overall smaller, less inequivalve, thinner shelled, and less rostrate than *Notocorbula* species. Odé (1976) listed *Notocorbula* among those taxa close to *Varicorbula* but needing clarification. We advocate continued use of *Varicorbula* and *Notocorbula* as separate genera until a more comprehensive study of the family, including examination of living animals, can be made (in agreement with Woodring, 1982; Anderson, 1996; Lamprell et al., 1998).

Flexicorbula Chavan, 1947 (based on *Varicorbula* (*Flexicorbula*) *vokesi* Chavan, 1947 [specimens not seen],

a Cretaceous fossil from Palestine, type by original designation) is probably synonymous with *Varicorbula*, the former being similarly inequivalve and bluntly rostrate. *Flexicorbula* was originally distinguished from *Varicorbula* by having prosogyrous beaks as well as a distinct lamella posterior to the hinge (a pseudo-lateral tooth, often termed P1) (Chavan, 1947). Observations on museum specimens of *V. gibba* and on the species discussed herein show that *Varicorbula* species are also prosogyrous and also possess a strong P1 (Figures 15, 16).

Vokesula Stenzel & Twining in Stenzel et al., 1957 (based on *Corbula smithvillensis* Harris, 1895, from Eocene to Oligocene of North America, type by original designation) also appears very similar (Stenzel et al., 1957:pl. 21, figs. 11–29, pl. 22, figs. 1–6; Keen, 1969:pl. E156, figs. 7a–c), except that the smaller left valve is nearly smooth (i.e., without radials?) and nepionic caps are clearly evident on both valves (although the original authors [Stenzel & Twining in Stenzel et al., 1957:173, 176] described a "neanic portion" yet claimed the umbones to be "generally not set off by a resting stage"). Odé (1976:28) also recognized the similarity, and likewise left it unresolved, noting only that the status of *Vokesula* relative to *Varicorbula* "needs to be clarified."

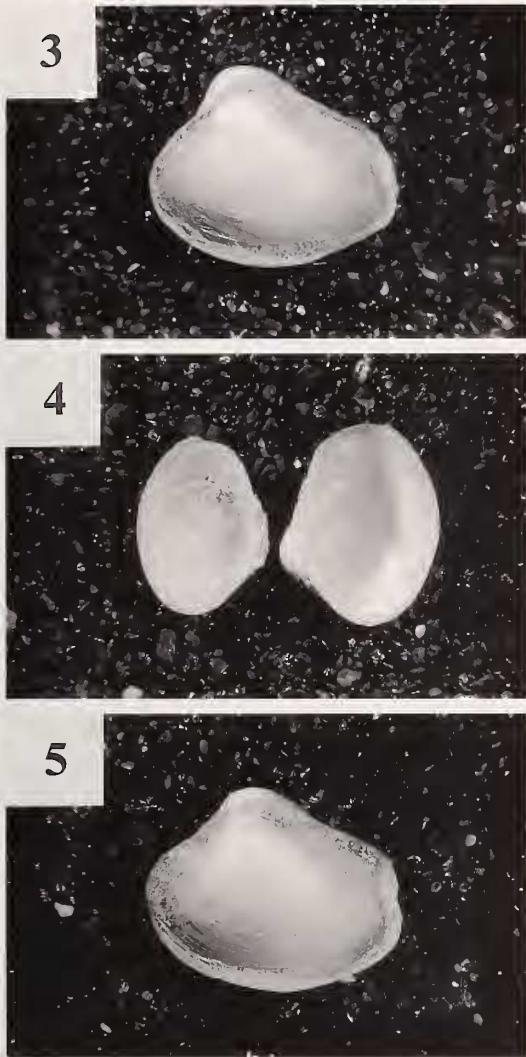
Caryocorbula Gardner, 1926 (based on *Corbula alabamiensis* Lea, 1833, from the western Atlantic Eocene, type by original designation), has been used by some authors without explanation for some of the species here under consideration (Johnson, 1934; McLean, 1936; Aguayo & Jaume, 1950; Abbott, 1974). *Caryocorbula* is characterized as only slightly inequivalve and similarly sculptured on the right and left valves (Gardner, 1926; Vokes, 1945; Stenzel et al., 1957). Its application to the species is perhaps due to mention of "a microscopically fine radial lineation" (Gardner, 1926: 46), which is however distinctly different from the radial ridges present in *Varicorbula*.

Varicorbula disparilis (d'Orbigny, 1842)

(Figures 1–25)

Selected synonymy:

- Corbula disparilis* d'Orbigny, 1842:pl. 27, figs. 1–4; 1853: 283 (sp. no. 484). Type locality: Guadeloupe.
- Corbula disparilis* d'Orbigny, 1846 [sic].—Dall, 1886:314–315, pl. 1, figs. 4, 4a, b; 1889:70, 71, pl. 1, figs. 4, 4a, b [after Dall, 1886].—McLean, 1951: 114, pl. 23, fig. 11 [after Dall, 1886].
- Corbula disparilis* d'Orbigny, 1853 [sic].—Dall, 1881:115. —Baker, 1965:105.
- Corbula disparilis* d'Orbigny.—M. Smith, 1937:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1940:120, sp. 1557, figs. a, b [after Dall, 1886]; 1941:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1945:67, pl. 60, figs. 4a, b [after Dall, 1886]; 1951:67, pl. 60, figs. 4a, b [after Dall, 1886].
- Corbula linatula* Conrad, 1846 (Feb.): 25, pl. 1, fig. 2. Type locality: Gulf of Mexico, off the coast of Florida.—

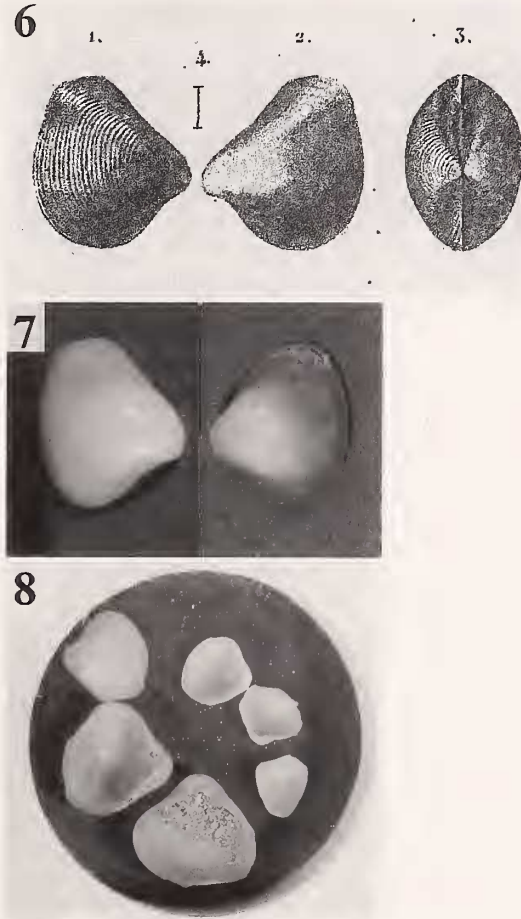


Figures 3–5. *Corbula limatula*, ANSP 50909, type material. Figure 3. Articulated paralectotype, 8.0 mm length. Figure 4. Disarticulated paralectotype, larger valve = 6.6 mm length. Figure 5. Articulated lectotype (ANSP 50909a), 8.3 mm.

Lamy, 1941:228 (remark only, within section *Cuneo-corbula*).—Baker, 1964:67 (lectotype designation); 1965:104–105.

Varicorbula operculata (Philippi, 1848).—Abbott, 1974: 538, text-fig. 5996 [after Dall, 1886].—Vokes & Vokes, 1984:45, pl. 47, fig. 7c only.—Lyons, 1989:61, pl. 18, figs. 1a, b.—Abbott & Morris, 1995:103, text fig. 33 [after Dall, 1886], pl. 23, fig. 11 bottom specimen only (color).

Diagnosis: *Varicorbula* of 5–9 mm shell length, whitish with persistent rose-colored margins dorsally. Radial ridges on left valve weak, restricted to anteroposterior slopes and near shell margins. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 42–46%.



Figures 6–8. *Corbula disparilis*. Figure 6. Original illustrations from d’Orbigny in Sagra, 1842. Scale bar (d’Orbigny’s fig. 4) = 5.4 mm. Figures 7, 8. Syntypic lot (BMNH 1854.10.4.550). Figure 7. Two largest valves: right valve (at left, lectotype here designated), 5.1 mm length; left valve (at right, not conspecific), 5.0 mm length. Figure 8. Other six valves; smallest (left) valve, 2.3 mm length.

Taxonomy: Although the species of the present material has been most often called *Varicorbula operculata* (Philippi, 1848) in the literature, an earlier name exists. *Corbula disparilis* d’Orbigny, 1842, described from Guadeloupe, has most often appeared as the senior synonym of the species names discussed here, based on the assumed date of publication (see below) (e.g., Bush, 1885a; Dall, 1886; Guppy & Dall, 1896; Dall & Simpson, 1901; Maury, 1920; Lamy, 1941; McLean, 1951; M. Smith, 1937, 1941, 1945, 1951; Anderson, 1996, with “?”; Lee, 2000). Some other authors (Pulley, 1953; Abbott, 1954, 1974; Rios, 1975, 1985, 1994; Jensen & Harasewych, 1986) have used *V. operculata* as the senior synonym, considering *C. disparilis* “of authors, non d’Orbigny,” as synonymous. Still other authors (Warmke & Abbott, 1961; Morris, 1973; Abbott & Morris, 1995) have listed *C. dis-*

parilis d'Orbigny in synonymy or as a previous name without further comment.

Baker (1965) noted that the original figures of *Corbula disparilis* show a decidedly subequivalve shell (d'Orbigny, 1842:pl. 27, figs. 1–3; reproduced in Figure 6), and concluded that it is most likely not conspecific with *Varicorbula operculata*. Dall (1886), however, considered d'Orbigny's figures inaccurate or based on separated valves without periostracum, because the original text description (d'Orbigny, 1853:283) indicated that the shells are inequivalve (also reflected by the etymology of the name). Examination of the syntypic lot of *C. disparilis* (BMNH 1854.10.4.550, *vidi*; Figures 7, 8) revealed that Dall was indeed correct and that Baker was not. This lot contains eight disarticulated valves (six right valves, two left valves), none of which are paired. The six small valves (five right; one left; 4.6–2.3 mm; Figure 8) assuredly belong to a species of *Varicorbula*. The five small right valves are somewhat thin-shelled, heavily sculptured, and have interior peripheral grooves for the edge of the smaller left valve; their truncation:height ratios vary widely (39–52%) across the range noted in *V. disparilis*, *V. krebsiana*, and *V. philippii* (see below), and are thus inconclusive. The small left valve (2.3 mm) lacks defining periostracum and radial ridges; it is thin-shelled and weakly sculptured but is otherwise uninformative.

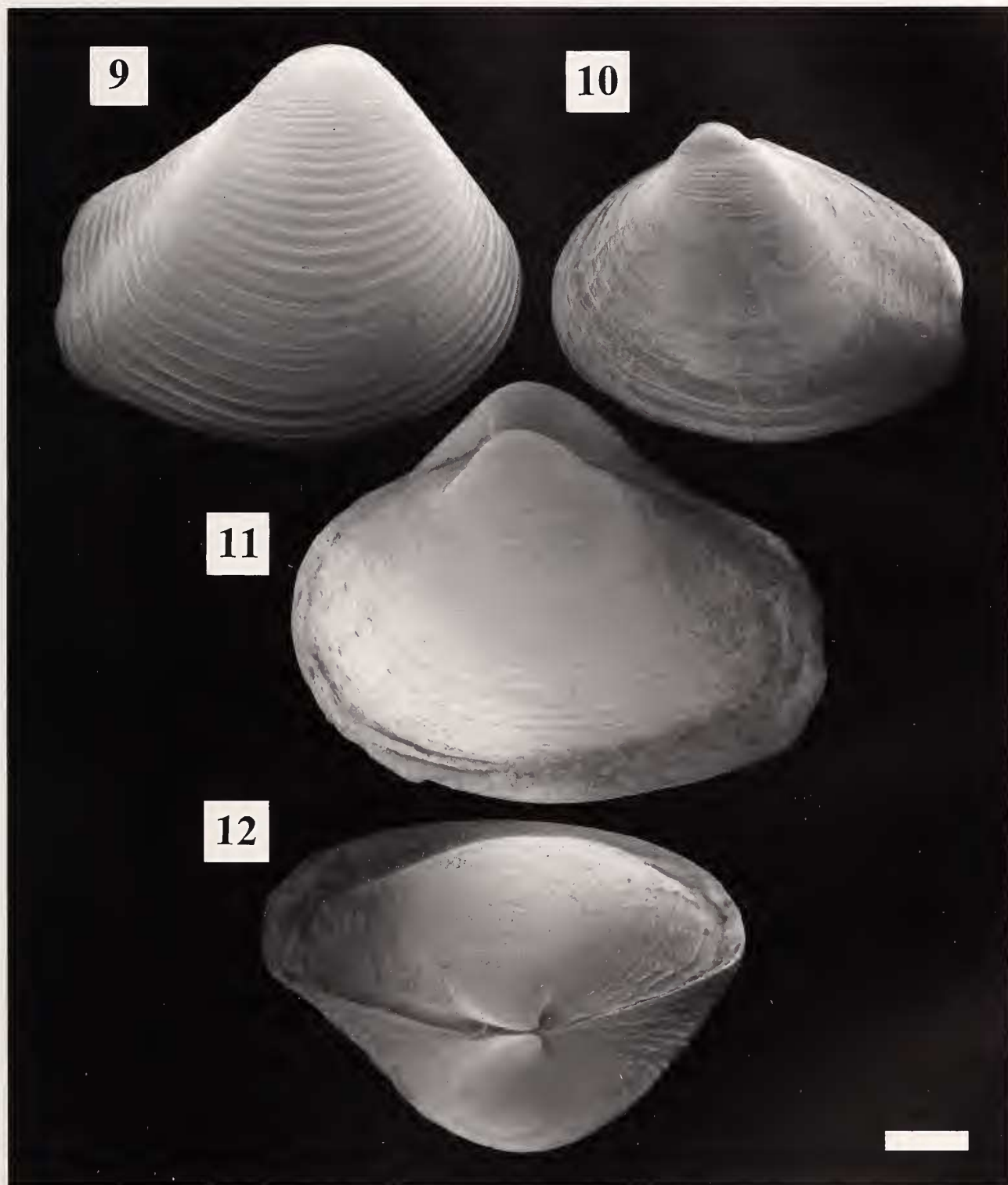
The two largest valves of the syntypic lot of *Corbula disparilis* (right valve 5.1 mm, left valve 5.0 mm length; Figure 7), however, appear to form a single nearly equivalent pair when viewed side-by-side; this is presumably what d'Orbigny's illustrator assumed. The large left valve (Figure 7, at right; probably also illustrated by d'Orbigny, 1842:pl. 27, fig. 2, reproduced in Figure 6) is thick-walled and stained black (the other seven valves are all whitish); it is not likely conspecific with the rest, nor (on the basis of sculpture) congeneric. The large right valve definitely belongs to a species of *Varicorbula*. It appears to be the right valve illustrated by d'Orbigny (1842:pl. 27, fig. 1; reproduced in Figure 6), and although it does not exactly match the published figure (which has a truncation:height ratio of 34%, too small for *C. disparilis*; see below), the latter probably suffers from the "artistic license" noted in other d'Orbigny figures (Mikkelsen & Mikkelsen, 1984: figs. 6C, D). Because this large right valve (Figure 7, at left) is also closest in size to the illustrated length bar (5.4 mm; d'Orbigny, 1842:pl. 27, fig. 4), we here designate this valve (5.1 mm; truncation:height ratio 45%) as the lectotype of *C. disparilis*. The six small valves are considered paralectotypes, but are acknowledged as being of problematic identification. The large left valve is here excluded from the syntypic series.

The original material of *Corbula limatula* Conrad, 1846, was interestingly similar to the present collections, being "dredged up on the sounding lead in deep water off the coast of Florida." The syntypic lot (ANSP 50909, *vidi*) contains three valve pairs (Figures 3–5), virtually

identical in morphology to those of the present collections (Figures 9–12) and to the lectotype of *Varicorbula disparilis*. Baker (1964) gave the "type" of *C. limatula* as ANSP 50909a, of 8.2 × 6.3 mm, an act that constitutes a lectotype designation. Although the three specimens of the ANSP lot have since been reunited, it is reasonable to assume the specimen closest to these stated dimensions (largest syntype, 8.3 × 6.6 mm; Figure 5) is the lectotype, and this has now been reseggregated as such. The remaining two syntypes can now be considered as paralectotypes. This species' yellow-and-pink shell coloration has a tendency to turn to white-and-brown in older collections, as mentioned in Conrad's (1846) description and as seen in other museum material (e.g., AMNH).

This discussion stops short of synonymizing *Corbula operculata* Philippi, 1848, with *Varicorbula disparilis*, although most previous authors have considered them conspecific, and it seems likely that this is true. Baker (1965) noted the closeness of *V. disparilis* [as *C. limatula*] with *C. operculata*, the latter described from St. Thomas, on mud at 15–18 fathoms. Philippi's (1848:13) description reads [our translation from the original Latin]: "shell heart-shaped triangular, very inequivalve, anteriorly subtruncated, white, right [*sic*] valve small, smooth, brownish, the left [*sic*] deeply transversely sulcated, the apex inrolled, the regions of the lunula and area brown." A search for the type material of this species was unsuccessful (not in Humboldt Museum, Berlin, M. Glaubrecht, in litt., July 1997; not in BMNH, J. D. Taylor and K. Way, in litt., February 1998; ?in Museo Nacional de Historia Natural, Santiago, Chile, no reply; ?in Übersee-Museum, Bremen, Germany, no reply). Because the unillustrated original description is inadequate to distinguish *V. operculata* from other western Atlantic species, and the only material from the Virgin Islands that we have seen is in fact *V. philippii*, synonymy cannot confidently be made without examination of type material. Until Philippi's original specimens can be located, *Corbula operculata* must be considered a *nomen dubium*.

The original publication dates of d'Orbigny's numerous western Atlantic bivalve descriptions in Sagra's *Histoire physique, politique et naturelle de l'Île de Cuba* are of considerable uncertainty. Although this controversy is not the prime subject of this report, its outcome determines the date of publication for *Corbula disparilis*, and thus the priority status of this name relative to *C. limatula* and *C. operculata*. For this reason, we here provide a brief summary of the evidence that has led us to consider *C. disparilis* as the oldest name. d'Orbigny's "Sagra Report" was originally published in French, and later translated into Spanish [as *Historia física política y natural de la Isla de Cuba*]. The former was issued in two volumes of text and one of plates, each apparently published in small installments (livraisons), the individual dates of which have never been definitively compiled. Volume 1 of the French edition dates from 1840/41–1842 and vol-



Figures 9–12. *Varicorbula disparilis*, FK-106, scanning electron micrographs. Figure 9. Larger (right) valve. Figure 10. Smaller (left) valve. Figures 11, 12. Articulated specimens. Scale bar = 1 mm (for 9–12).

ume 2 from 1842–1853 (Aguayo, 1943; G. Rosenberg, personal communication).

Three dates have been given for *Corbula disparilis* d'Orbigny in the literature: 1842, 1846, and 1853. The text description for *C. disparilis* (vol. 2, p. 283) was almost certainly published in 1853, but if (as certain authors claim) the Atlas pages on which this species was named and figured (pl. 27, figs. 1–4; making the name taxonomically available) were published earlier, the date would derive from that of the Atlas. A number of authors (Dall, 1885; Aguayo, 1943 [citing earlier authors]; Petit & Harasewych, 1990) have claimed that the French atlas appeared in 1842 (as a unit rather than livraisons), concurrent with the completion of volume 1, and indeed this is the date most frequently applied to the various bivalves of d'Orbigny (e.g., Abbott, 1974; Turgeon et al., 1998). 1853 is the latest date by which all of d'Orbigny's French work, text or plate pages, would have been published. This is the date applied to *C. disparilis* by Dall (1881), Baker (1965), and G. Rosenberg (personal communication), and as previously mentioned is probably the date of the text description. Some of the *Corbula* species in this volume are referenced as "d'Orb. 1846" (referring to the Spanish edition? see below) while others (including *C. disparilis*) are given merely as "d'Orb."; this implies that the text indeed appeared later than 1846. As evidence in support of 1853 for *C. disparilis*, Baker (1965) noted that none of d'Orbigny's *Corbula* species were covered by C.B. Adams (1852); the earliest citation of d'Orbigny's bivalves located by G. Rosenberg (personal communication) is Mörch (1852), which lacks d'Orbigny's *Corbula* species as well. The date 1846 as used by some authors apparently derives from the appearance of *C. disparilis* in the Spanish edition, published as a single volume. Because the French text for *C. disparilis* likely dates from 1853, either the year 1846 is incorrect or (more likely) the Spanish translation predates the original French (?produced from the unpublished French manuscript). Based on the above uncertainties, we conservatively consider the publication date of *C. disparilis* as 1842, but note, in the event that subsequent research determines a later date, that *C. limatula* Conrad, 1846, could gain seniority as the earlier name.

The geologic range of *Varicorbula disparilis* extends back into the Middle Cenozoic. Maury (1920) considered it as Pliocene to Recent, but presented data only for the Pleistocene. Other Tertiary reports are the Mio/Pliocene of Panama and Costa Rica (Woodring, 1982), the Mio/Pliocene of Trinidad (Jung, 1969; as *Notocorbula* cf. *disparilis*), the Tertiary of the Dominican Republic (Gabb, 1873) and the Oligocene of Jamaica (Guppy & Dall, 1896).

Several additional names have been introduced for members of this group in the Cenozoic western Atlantic: *Corbula vieta* Guppy, 1866 (Trinidad, Jamaica); *Erycina tensa* Guppy, 1866 (Trinidad); *C. isla-trinitatis* Maury,

1925 (Trinidad, Panama, Venezuela); *C. (Varicorbula) heterogena* Guppy in Dall, 1898 (Jamaica); *C. (V.) sanctidominici* Maury, 1925 (Dominican Republic); *V. sanctianderaea* Maury, 1925 (Trinidad); *V. baea* Woodring, 1982 (Panama); *V. waltonensis* Gardner, 1928 (Florida); *C. (Aloidis) caloosae* Dall, 1898 (Florida); *V. chipolana* Dall in Gardner, 1928 (Florida); *C. (Notocorbula) bruscasensis* Weisbord, 1964 (Venezuela); *C. (N.) puntagordensis* Weisbord, 1964 (Venezuela); *V. chowanensis* Bailey, 1977 (North Carolina). Although many of these have been compared with *V. disparilis* or its synonyms and congeners discussed herein (Gabb, 1873; Guppy & Dall, 1896; Dall, 1898; Maury, 1917; Olsson & Harbison, 1953; Anderson, 1996), they have not been critically re-examined here. Even if any of these are ultimately found conspecific with *V. disparilis*, this would not change the earliest name of the extant taxon.

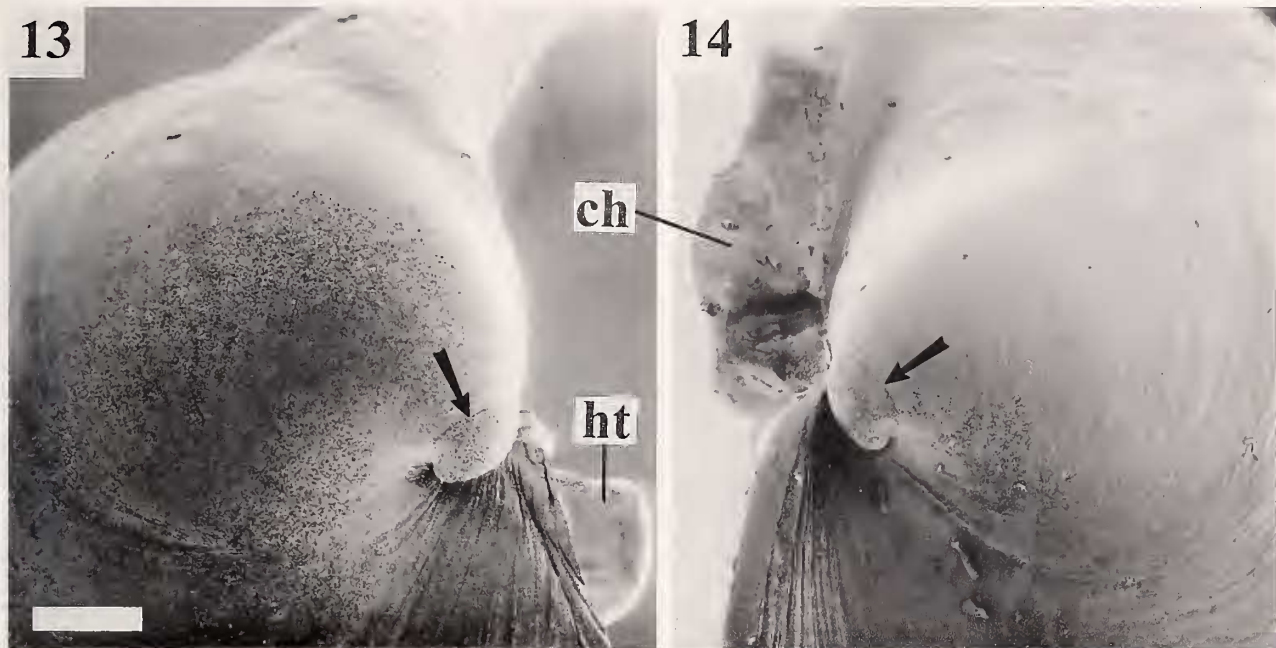
Shell: The shell of *Varicorbula disparilis* (Figures 9–12) ranges from 5–9 mm in length (larger valve measured; min. = 4.6, max. = 8.7, mean = 6.6 ± 0.8 SD [standard deviation], $n = 100$). In life the shell is whitish with a light yellow blush (especially at the umbones), and dorsal rose-colored margins to either side of the umbones, and usually also on the posterior slope of the smaller left valve; empty shells are white with persistent rose margins.

The prodissoconch (Figures 13, 14) is composed of a small embryonic shell (prodissoconch I) of ca. 200 μ m diameter, separated from the larger larval shell (prodissoconch II) by a distinct growth line, indicative of planktic development. The larval shell is ca. 1.5 mm in anteroposterior length and is separated indistinctly from the dissoconch, only by a change in sculpture from smooth to concentrically sculptured.

The inner surface of the valves (Figure 15) has anterior and posterior adductor muscle scars joined by an evenly curved pallial line. Posteriorly the pallial line is sharply angled, forming a shallow embayment (pallial sinus) for the siphons. The posterior scar is broadly oval; the anterior is elongated crescent-shaped; smaller pedal retractor muscle scars abut each adductor scar dorsally near the hinge line. The hinge teeth (Figures 13, 14, 16) and chondrophore (Figure 14) are as described for the genus *Varicorbula* (above).

When closed, the two valves form a tight seal, without gaping, facilitated by the overlapping periostracum of the smaller valve and the peripheral groove for the edge of the smaller valve on the interior surface of the larger valve. Some specimens show calcification of the marginal periostracum on the left valve in the region of the siphons.

Anatomy: Only minor differences were noted here in the soft-body anatomy of *Varicorbula disparilis* (Figures 17–21) versus those reported for *V. gibba* by Yonge (1946) and *Corbula crassa* Hinds, 1843, by Morton (1990).



Figures 13, 14. *Varicorbula disparilis*, FK-106. Prodissoconch, showing distinct growth line (arrows) between prodissoconch I and II. Figure 13. Right (larger) valve, also showing hinge tooth (ht). Figure 14. Left (smaller) valve, also showing chondrophore (ch). Scale bars = 200 μ m (for 13 and 14).

The posterior mantle is heavily pigmented with opaque white in a thick "collar" surrounding the short incurrent and excurrent siphons; a brownish interrupted line (persistent after preservation) outlines the combined siphonal openings at the rim. Both siphons are papillate at the margin (Figure 18); the dorsal (excurrent) siphon is edged by a thin flap of tissue presumably forming an apical cone in life (as shown for *Varicorbula gibba* by Yonge, 1946: fig. 5). The remaining mantle edges are fused except for the pedal opening (from just ventral to the anterior adductor muscle to mid ventrally, just behind the heel of the foot), which is also papillate.

The adductor muscles are subequal, with the posterior more rounded and slightly larger. Each is distinctly formed of two parts (presumably "slow" and "quick" components, *vide* Yonge, 1946, and Morton, 1990). Small pedal retractor muscles lie dorsomedial and adjacent to each adductor. There is no pedal protractor muscle anteriorly.

The ctenidia (Figures 20, 21) are nonplicate, homorhabdic, and consist of smaller outer and larger inner demibranchs. Both demibranchs have sparse interlamellar junctions. The labial palps are long and narrow, comprising an inner pair on the anterior surface of the visceral mass, and an outer pair attached to the mantle near the anterior adductor muscle. The inner ctenidial demibranchs terminate anteriorly between the pairs of palps (Category III ctenidium-palp junction of Stasek, 1963) in the vicinity of the mouth. The demibranchs attach pos-

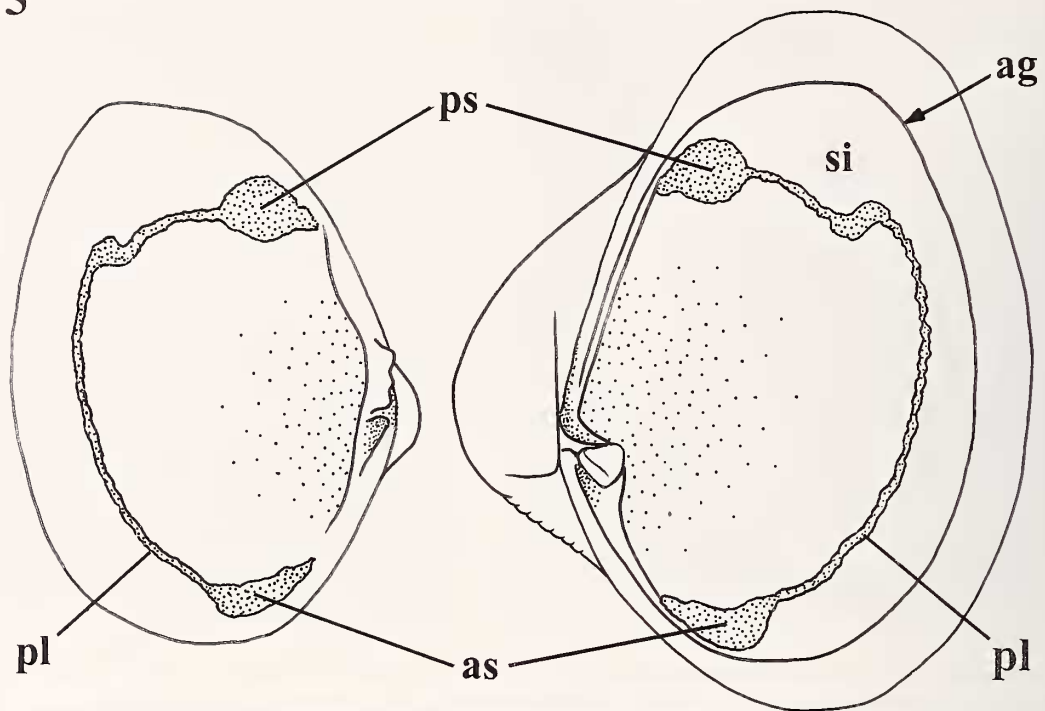
teriorly to the inner membrane between the incurrent and excurrent siphons.

The foot (Figure 19) is narrow, finger-shaped to compressed, translucent white, with an opaque white spherical byssal gland visible through the integument at the "heel." A ventral pedal groove, lined by mucus glands, extends from near the tip to the heel (where the byssal thread emerges). Only single byssal threads are produced.

The stomach (Type 5 of Purchon, 1987) occupies the visceral mass, surrounded by whitish gonad and darker digestive gland tissue. The esophagus opens dorsally into the anterior chamber; there is a wide opening to the digestive gland ventrally (actually three adjacent but separate openings according to Purchon, 1960: fig. 17). The posterior part of the stomach includes a large style sac, equipped at the dorsal end with a brownish gastric shield. The midgut conjoins the style sac and parallels its length, emerging from the ventral end of the sac as the intestine. The intestine undergoes a single loop within the gonad (Figure 17; apparently differing from that in *Corbula crassa*, described as having a "series of loops," Morton, 1990: 1067, fig. 14), its typhlosole persisting only until the anteriormost curve of the loop, where it then passes dorsally behind the stomach. The intestine exits the visceral mass posterodorsally, passes through the heart and kidney, over the posterior adductor muscle, and terminates at the anus just dorsal to the excurrent siphon.

Ganglia of the nervous system include small paired cerebral ganglia in the vicinity of the labial palps, a single

15



16



Figures 15, 16. *Varicorbula disparilis*, FK-106. Figure 15. Inner surface of valves (diagrammatic) showing hinge, muscle scars, pallial line, pallial sinus, and groove in the larger (right) valve for articulation of the smaller (left) valve. key: ag, articulation groove; as, anterior adductor muscle scar; pl, pallial line; ps, posterior adductor muscle scar; si, pallial sinus. Figure 16. Hinge, scanning electron micrographs of smaller (left) valve and larger (right) valve. Scale bar = 500 μm (for both views in 16).

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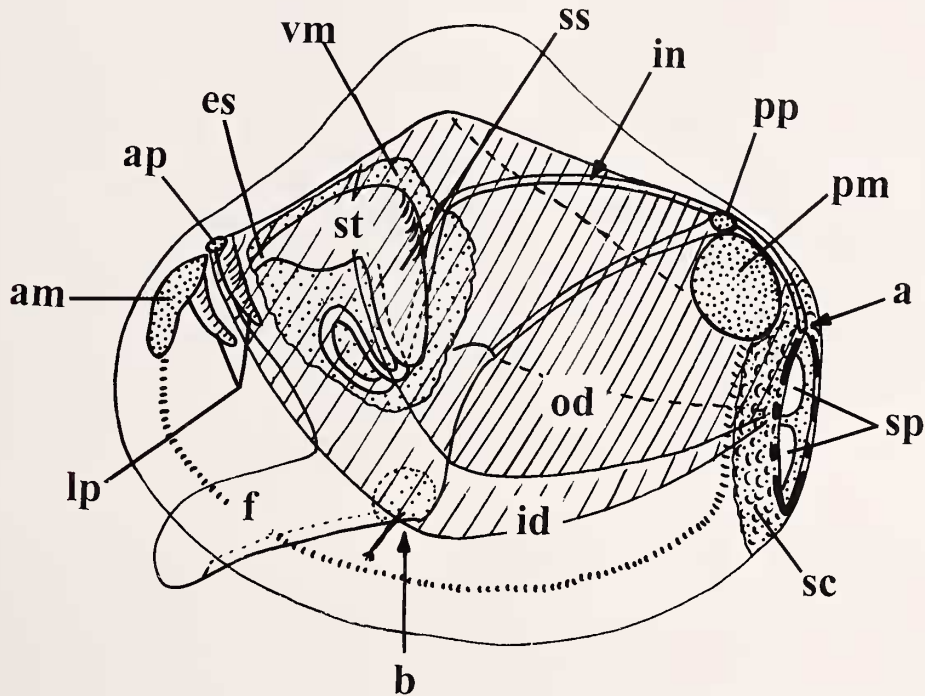


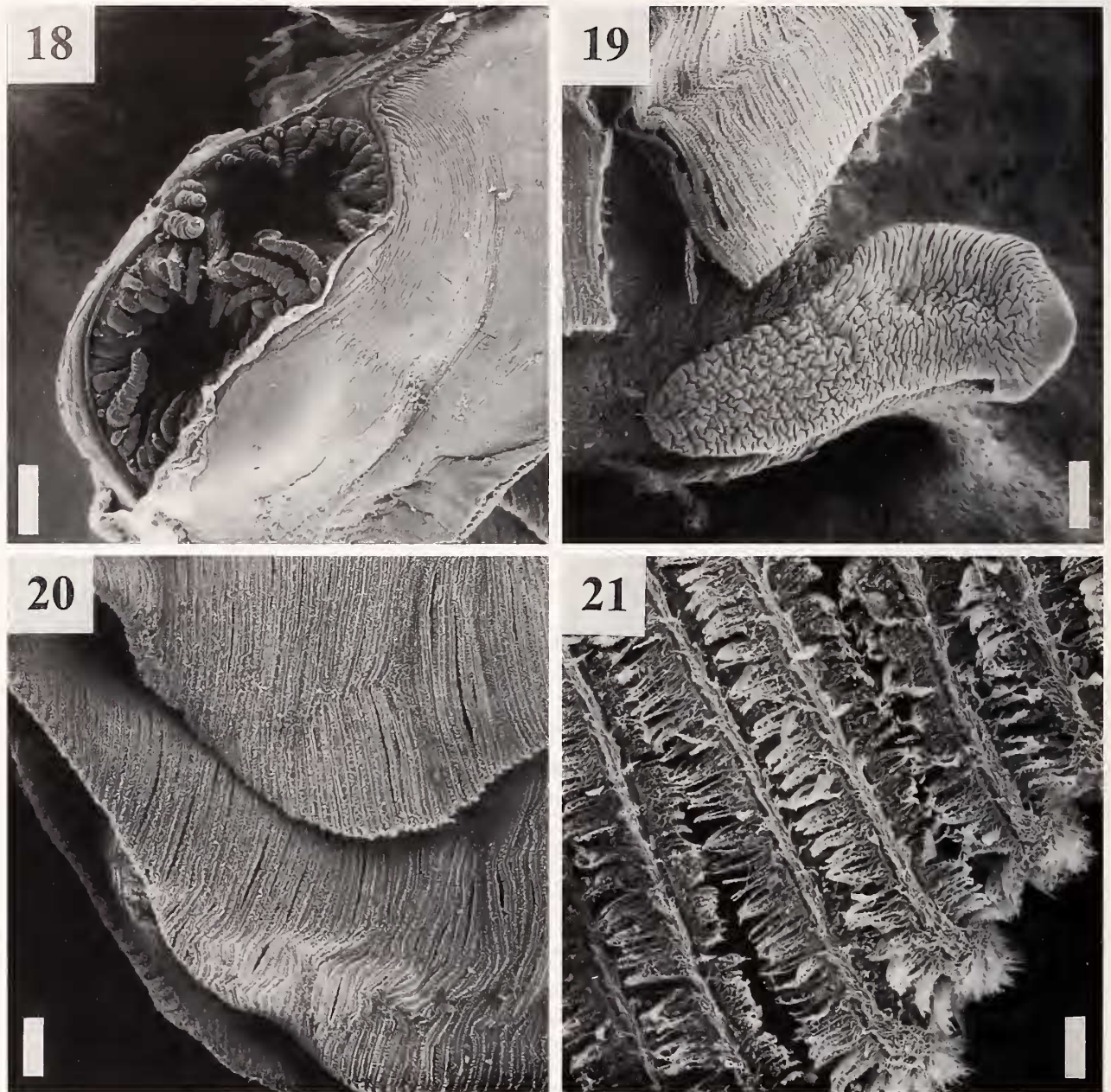
Figure 17. *Varicorbula disparilis*, diagrammatic gross anatomy. a, anus; am, anterior adductor muscle; ap, anterior pedal retractor muscle; b, byssal gland + byssus; es, esophagus; f, foot; id, inner demibranch of ctenidium; in, intestine; lp, labial palp; od, outer demibranch of ctenidium; pm, posterior adductor muscle; pp, posterior pedal retractor muscle; sc, siphonal collar; sp, siphons; ss, style sack; st, stomach; vm, visceral mass (gonad + digestive diverticula).

pedal ganglion in the muscle of the foot, just ventral to the gonad containing the intestinal loop, and a single visceral ganglion in the connective tissue anteroventral to the posterior adductor muscle.

Sexes are separate. Of the two specimens histologically sectioned, one contained only ova in the gonad, while the other contained only sperm. In addition to the presence of interlamellar junctions, there was no additional evidence of brooding (in the form of embryos in the gills).

Distribution: The published geographical distribution of *Varicorbula disparilis* (as *V. operculata* or *V. limatula*) most commonly includes at least the southeastern United States, the Gulf of Mexico, and the West Indies (e.g., Dall, 1889; Johnson, 1934; Warmke & Abbott, 1961; Abbott, 1974; Merrill et al., 1978). However, our observations of museum collections indicate that up to three species have been combined under the single species name. Therefore, all published references and localities require verification either through published figures or, preferably, museum specimens. Verified localities for *V. disparilis* (through specimens or recognizable published figures)

include (Figure 22): North Carolina (NCSM/IMS; Bush, 1885a, b; Dall, 1886, 1889; Maury, 1920; Johnson, 1934; M. Smith, 1937, 1941, 1945, 1951; Aguayo & Jaume, 1950; Abbott, 1954, 1974; Morris, 1973; Porter, 1974; Porter & Wolfe, 1971; Merrill et al., 1978; Abbott & Morris, 1995); South Carolina (NCSM/IMS; Porter, 1975); Georgia (NCSM/IMS; Dall, 1889); Florida, off eastern coast from St. Lucie County to Miami (AMNH, ANSP, FMNH, HBOM; McGinty & Nelson, 1972; Lyons, 1989; Lee, 2000), and the Florida Keys (AMNH, ANSP, HMNS, SBMNH, FK stations [Table 1]; Dall, 1881; Vittor, 1998); Gulf of Mexico, off western Florida from Boca Grande through Destin (Florida panhandle) (AMNH, ANSP, DMNH, FMNH; Maury, 1920; Gundersen, 1998), Alabama (HMNS; Shelton, 1997), Mississippi (Bock & Moore, 1968), Louisiana (ANSP, HMNS), Texas (HMNS; Odé & Spears, 1970; Treece, 1979); the Bahamas (AMNH), Guadeloupe (BMNH 1854.10.4.550 [types]; d'Orbigny, 1853), and Yucatan (Dall, 1881; Vokes & Vokes, 1984). Localities that have not been verified are: Virginia (Merrill et al., 1978), Cuba (d'Orbigny, 1853; Dall,



Figures 18–21. *Varicorbula disparilis*, details of anatomy, scanning electron micrographs of critical-point dried animals. Figure 18. Siphons; excurrent (dorsal) at upper right. Figure 19. Foot. Figure 20. Gills (posterior at left). Figure 21. Gill filaments. Scale bars = 20 μm (21), 200 μm (18, 19, 20).

1881, 1885, 1886; McLean, 1936; M. Smith, 1940; Aguayo & Jaume, 1950; Espinosa et al., 1994), Dominican Republic (Dall, 1885), Virgin Islands (Dall, 1881), Barbados (Dall, 1881), Martinique (d'Orbigny, 1853), Venezuela (Aguayo & Jaume, 1950), and Barbados (Dall, 1886, 1889; Maury, 1920). *Varicorbula disparilis* has likewise not been verified from Puerto Rico (Dall & Simpson, 1901; McLean, 1951; Warmke & Erdman,

1963) or Jamaica (d'Orbigny, 1853); all specimens seen thus far from Puerto Rico (AMNH, ANSP; Warmke & Abbott, 1961; text-fig. 31h) and Jamaica (AMNH, ANSP, DMNH, MCZ; C. B. Adams, 1852; Cockerell, 1894) are *V. krebsiana* (see below). Likewise, all known records from Grand Cayman (ANSP; Abbott, 1958), the Dominican Republic (AMNH), Haiti (E. A. Smith, 1885), the Virgin Islands (DMNH; Weber, 1961), Bermuda (DMNH;



Figure 22. Verified geographical distribution of *Varicorbula disparilis* (solid circles), *V. krebsiana* (x, Jamaica and Puerto Rico only), and *V. philippii* (open triangles).

E. A. Smith, 1885; Dall, 1889; Aguayo & Jaume, 1950; Waller, 1973; Jensen & Harasewych, 1986), and Brazil (Aguayo & Jaume, 1950; Rios, 1975, 1985, 1994) are *V. philippii* (see below). One published figure of a *Varicorbula* in the western Atlantic literature appears entirely incorrect: Morris' (1973: pl. 31, fig. 8) illustration of *Notocorbula operculata* shows an equivalve clam with no recognizable sculpture.

In summary, according to the known species distributions thus far, *Varicorbula disparilis* borders the continental coastline of the eastern United States and Gulf of Mexico. Although *V. philippii* overlaps much of this range (see below), it is also found in Bermuda and Caribbean locations (Belize, Greater and Lesser Antilles, Brazil). *Varicorbula krebsiana* is so far restricted to Jamaica and Puerto Rico.

Ecology: *Varicorbula disparilis* can be classed as a relatively deep-water continental-shelf species with recorded depths often exceeding 200 m (AMNH; Dall, 1881:127 and 450 fms = 232 and 823 m; Dall, 1881, 1886, 1889: 805 fms = 1473 m; Merrill et al., 1978: 475 m; Abbott, 1974:250 fms = 457 m). However, its range of depth is notable (Humfrey, 1975); very shallow depths (< 10 m) have also been recorded (Dall, 1889: 5 fms = 9 m; Mer-

rill et al., 1978: 9 m; Lyons, 1989: 7.1 m). Collections verified as live-collected are from 16.5–91.5 m (AMNH, HBOM, HMNS, NCSM/IMS; FK stations [Table 1]; Porter, 1975). Bottom type is either sand or mud (NCSM/IMS; FK stations [Table 1]; Porter, 1975). It has been recorded from the gut contents of bottom-feeding starfish (*Astropecten duplicatus* Gray, 1840) off North Carolina (Porter & Wolfe, 1971; as *V. operculata*, vouchers NCSM-IMS), and bottom-feeding bonefish [*Albula vulpes* (Linnaeus, 1758)] off Puerto Rico (Warmke & Erdman, 1963; as *Notocorbula operculata*, unverified).

Corbulids are well known for organic conchiolin layers within the matrix of the calcareous shell, presumably protecting the bivalve from chemically boring predators and shell dissolution in deep and/or cold calcium-carbonate-deficient waters (Lewy & Samtleben, 1979; Morton, 1990; although Anderson et al. [1991] showed that other factors [e.g., size] might be more important against predation). Both complete and incomplete boreholes have been noted in the material examined herein (FK-98, FK-104; AMNH 273274, HMNS 7345). Some of these boreholes are distinctly bevelled, while others are straight-sided, suggesting several predator species (e.g., Naticidae, Muricidae). The conchiolin layer has also been viewed as a "gasket" to seal the edge of the smaller left valve into the groove of the larger right valve, to the extent that presence of the internal groove alone was interpreted as evidence of conchiolin in fossilized species by Lewy & Samtleben (1979).

Population structure: Thirty-five living specimens were obtained in the FK-104 Shipek grab sample. Based on the grab's surface area of ca. 1 ft² (=0.093 m²), population density at this location can be estimated at 376 individuals/m². Within this quantitative sample, shell length of the larger right valve ranged from 4.8 to 7.8 mm (mean = 6.4 ± 0.7 SD, n = 35). A random sample of specimens from the trawl sample (FK-106) was similar (range 4.6–8.7 mm, mean = 6.7 ± 0.8 SD, n = 65).

The catch of the trawl sample (FK-106) was limited to common shallow water fishes and crustaceans. The "tickle chain" sample contained an estimated 3200 living specimens of *Varicorbula disparilis* entangled within the mat. Also present were a few living individuals of mussels (*Amygdalum politum* Verrill & Smith, 1880), single living specimens of the jingle shell (*Anomia simplex* d'Orbigny, 1842) and a second corbulid (*Corbula caribaea* d'Orbigny, 1842), plus empty shells of various bivalves [*Gouldia cerina* (C. B. Adams, 1845), species of *Nuculana*, *Anadara*, Tellinidae, and Lucinidae], gastropods [*Acteocina bidentata* (d'Orbigny, 1842), species of *Calyptraea*, *Olivella*, Turridae, and Pyramidellidae], and fragments of sea urchins and barnacles.

Numerous *Varicorbula* specimens in FK-106 served as substratum to other attached mollusks (Figures 23–25). The most common is a species of Arcidae (2.6–6.1 mm,



Figures 23–25. *Varicorbula disparilis*, FK-106, specimens with attached mollusks. Figure 23. *Anadara* cf. *floridana*, attached to a 7.0 mm *V. disparilis*. Figure 24. Distribution of attached mollusks ($n = 75$) on *V. disparilis* shells ($n = 41$). Solid circles = *A. cf. floridana* (or its byssus); solid squares = *Arcinella cornuta*; open circles or squares = attachment of respective attached mollusks on other side of shell. Figure 25. Nealagic *A. cornuta*, attached to a 7.2 mm *V. disparilis*.

mean 4.1 ± 1.1 SD, $n = 10$; Figure 23), byssally attached to the *Varicorbula* most often (82%) on the smaller left valve. Distribution of attachment (evidenced by attachment site of byssal threads [$n = 72$] on 38 individual *V. disparilis*; maximum six attachments/clam) was more often on the posterior dorsal or ventral quadrants, but also occurred near the anterior end and at the center of the valves (Figure 24, circles). Larger empty specimens (up to 25 mm shell length) of this same form were also collected in most of the Shipek grabs listed in Table 1. The arcid species is clearly a member of *Anadara*—inequi-

valve, inequilateral, moderately compressed, with a long straight hinge line, dark periostracum (hairy between the ribs, in dark concentric bands posteriorly), ca. 30 radial ribs (nodulose anteriorly), and a median radial indentation in the very early growth stage. Of the western Atlantic species, it is closest to *Anadara floridana* (Conrad, 1869), although that species has a much larger “adult” size (8–10 cm) which has not been collected or otherwise seen from the Florida Keys in this study.

Three other *Varicorbula* specimens each have a small (2.1–3.3 mm, mean 2.7 ± 0.5 SD) attached specimen of a species of Chamidae (Figure 25), barely past the prodissoconch stage. The chamid’s prodissoconch is smooth, orange or cream (one with radial pink rays), with widely spaced, thin, raised concentric ridges. The first growth of teleoconch has ruffled sculpture. Attachment to *Varicorbula* is near the posterodorsal hinge line (Figure 24, squares), cemented by the right valve of the chamid. By comparison with very small specimens of other western Atlantic Chamidae species, the form is attributable to *Arcinella cornuta* Conrad, 1866 (e.g., FMNH 164927, Gulf of Mexico, dredged, 1962 Smith!, Goodwin Collection #1869, 2 specimens; see also Nicol, 1952:figs. 1–12, as *Echinochama*), a species also known from off eastern Florida, Key Largo, the Lower Florida Keys, the Gulf of Mexico, and the West Indies.

Byssal mat: The mat which entangled the clams to the trawl’s “tickle chain” was composed of byssus fibers plus long gelatinous egg strings covered with sand grains and shell fragments, along with filamentous algae and branching Bryozoa. The *Varicorbula* clams were byssally attached to the mat material when collected. Some byssal threads reached several times the shell length. The egg string is tubular, round in cross-section, 0.5 mm in diameter (after preservation), containing two rows (or a very tight coil?) of eggs, each in more or less spherical capsules (160–190 μm in diameter, not interconnected by chalazae), 115–125 per cm. All eggs were at in the same stage of development (unshelled, multicellular).

This mat of byssal threads and egg strands with which so many specimens of *Varicorbula limatula* were collected could be interpreted as a byssal “nest” (although none of the smaller Shipek grab samples confirmed this). While other bivalves are known to produce byssal mats (e.g., certain mytilids and limids; Thorson, 1935; Fisher, 1936; Merrill & Turner, 1963; Morton, 1974), these typically encase the clam against a solid substratum. Byssal nests are thought to provide special protection to a thin-shelled adult, or to brooded larvae (Merrill & Turner, 1963); in *Varicorbula*, heavy byssal production, even though non-enveloping, could serve to more firmly anchor epibenthic individuals to rubble or sand particles (as in *Musculista*; Morton, 1974). It seems certain that more byssal production was involved here than a single byssal

thread per clam, attached to a below-sediment particle, as depicted for *V. gibba* by Stenzel et al. (1957:fig. 6).

It was initially tempting to speculate that the egg strands collected in the FK-106 sample were those of *Varicorbula disparilis*. A few other bivalve species are known to produce eggs in external strands or capsules [e.g., *Musculus discors* (Linnaeus, 1767), *Turtonia minuta* (Fabricius, 1780); see Thorson, 1935; Oldfield, 1955, 1964]. However, the available data for these egg strands and *V. disparilis* are inconclusive: (1) the encapsulated larvae were unshelled at the time of collection; (2) despite repeated trials, staff in the AMNH Invertebrate Molecular Systematics Laboratory were unable to extract DNA from the eggs for comparison with that of the adult clams (probably due to inadequate preservation; G. Giribet, personal communication); (3) multicelled embryos in the egg strands are 170 μm diameter (prodissoconch I is 200 μm diameter); eggs in ovarian follicles of the single sectioned female are a magnitude smaller (16–20 μm diameter), but this could merely indicate an early developmental stage (Morse & Zardus, 1997); and (4) no accessory glandular structures were found in sectioned specimens (such as the thickened mantle edges postulated to secrete the saclike egg capsules in *T. minuta*; Oldfield, 1955, 1964). Other mollusks occurring in the area are known to produce superficially similar egg strands (most especially, *Strombus* spp.; Robertson, 1959), and we cannot rule these out as the source. The association of *V. disparilis* with this byssal/egg mat is nevertheless intriguing, and is presented here for future reference.

Varicorbula krebsiana (C. B. Adams, 1852)

(Figures 22, 26)

Selected synonymy:

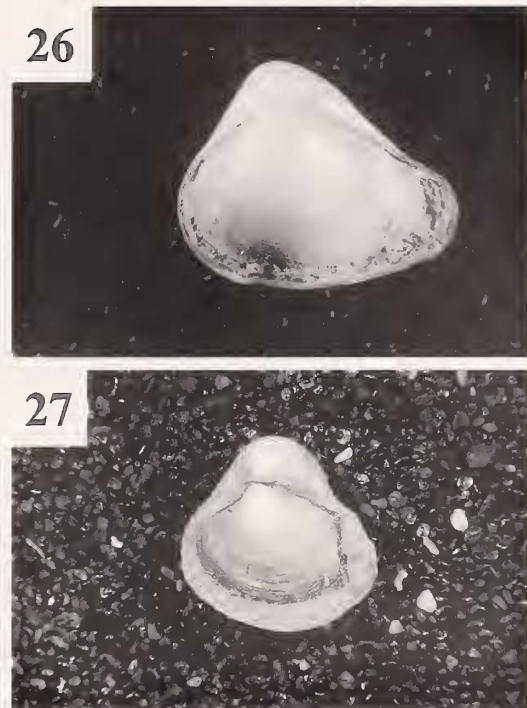
Corbula krebsiana C. B. Adams, 1852:234. Type locality: Jamaica.—Dall, 1886: 315, 316, pl. 1, figs. 1, 1a, b; 1889:70, 71, pl. 1, figs. 1, 1a, b [after Dall, 1886].—Clench & Turner, 1950:300, pl. 48, fig. 3.—Abbott, 1974:539, text-fig. 6011 [after Dall, 1886].

Corbula krebsiana C. B. Adams.—M. Smith, 1937:67, pl. 60, figs. 1a, b [after Dall, 1886]; 1940:120, sp. 1559, figs. a, b [after Dall, 1886]; 1941:67, pl. 60, figs. 1a, b [after Dall, 1886]; 1945: 67, pl. 60, figs. 1a, b [after Dall, 1886]; 1951: 67, pl. 60, figs. 1a, b [after Dall, 1886].

Notocorbula operculata Philippi, 1848 [*sic*].—Warmke & Abbott, 1961: text-fig. 31h.

Diagnosis: *Varicorbula* of 3–5 mm shell length. Radial ridges on left valve weak. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 35–39%.

Remarks: *Corbula krebsiana* C. B. Adams, 1852, described from Jamaica, is very similar to *Varicorbula disparilis*, including in coloration (“often tinged with pink”;



Figures 26, 27. Figure 26. *Varicorbula krebsiana*, MCZ 115611, Jamaica, lectotype, 6.1 mm length. Figure 27. *Varicorbula philippii*, AMNH 128166, off Palm Beach County, Florida, 6.4 mm length.

C. B. Adams, 1852:234). It was placed in synonymy with *V. operculata* by Rios (1970, 1975, 1985, 1994), without further explanation; C. B. Adams (1852:234) stated that it “probably . . . resembles *C. operculata* Phil.” and Andrews (1981a, b, 1992, 1994) listed it as a possible synonym. The type specimens of *C. krebsiana* (lectotype: MCZ 155611 [Dall, 1886:pl. 1, figs. 1, 1a, b; right valve only figured by Clench & Turner, 1950:pl. 48, fig. 3; Figure 26]; paralectotypes: MCZ 155612, DMNH 21941, ANSP 297148, ANSP 182624; see also Mikkelsen & Bradford, 1997) are overall smaller and more posteriorly pointed than typical *V. disparilis*. That is, in comparably sized specimens (3–5 mm length), the truncation:height ratio is smaller in *C. krebsiana* (35–39%, $n = 4$; also evident in illustrations by Dall [1886: pl. 1, figs. 1, 1a, b], and Warmke & Abbott [1961:text-fig. 31h]) than in *V. disparilis* (42–46%, $n = 4$). Dall (1886) maintained it as distinct on the basis of its “more delicate” (= smaller) form; others (Tryon, 1869, with “?”; Cockerell, 1894; Johnson, 1934; Lamy, 1941; M. Smith, 1937, 1941, 1945, 1951; Weisbord, 1964; Abbott, 1974; Odé, 1976) have agreed. In the absence of additional evidence, we maintain this species as valid within *Varicorbula* pending further data.

Although Dall (1889) included Cape Florida and the Florida Keys in its distribution (also M. Smith, 1937,

1940, 1945; Aguayo & Jaume, 1950; Abbott, 1974), we have seen specimens only from Jamaica (AMNH, ANSP, DMNH, MCZ) and Puerto Rico (AMNH, ANSP, FMNH) (Figure 22). Warmke & Abbott's material from Puerto Rico, based on their illustration (Warmke & Abbott, 1961:text-fig. 31h, as *Notocorbula operculata*), appears to be *V. krebsiana*; other Puerto Rican records (Dall & Simpson, 1901; Warmke & Erdman, 1963) cannot be verified in the absence of an illustration or voucher material. Its occurrence in Cuba (Aguayo & Jaume, 1950) is also unverified. Its depth range is usually deep, although shallow-water collections have also been noted (Dall, 1889: 3–85 fms [5.5–155.5 m]; this study 5.5–7 m [MCZ]); none of these records is, however, based on verified living populations.

Varicorbula philippii (E. A. Smith, 1885)

(Figures 22, 27)

Selected synonymy:

- Corbula philippii* E. A. Smith, 1885:33–34, pl. 8, figs. 4–4b.
Aloidis operculata (Philippi, 1849 [sic]).—Pulley, 1953: 197–198, pl. 18, fig. 17.
Corbula (*Varicorbula*) *operculata* Philippi, 1849 [sic].—Rios, 1975:251, pl. 80, fig. 1205; 1985:270, pl. 94, fig. 1334; 1994:292, pl. 99, fig. 1427.
Corbula (*Varicorbula*) *operculata* (Philippi, 1849 [sic]).—Andrews, 1981a:140, text-fig.; 1981b:140, text-fig.; 1992:140, text-fig.; 1994:145, text-fig.
Varicorbula operculata (Philippi).—Jensen & Harasewych, 1986:488–489, fig. 162.
Varicorbula operculata (Philippi, 1848).—Abbott & Morris, 1995:pl. 23, fig. 11 top specimen only (color).—Vokes & Vokes, 1984:pl. 47, figs. 7a, b only.
Corbula krebsiana C. B. Adams, 1852.—Andrews, 1971: 216–217, text-figs.
Corbula cf. *krebsiana* C. B. Adams, 1852.—Andrews, 1977: 251, text-figs.

Diagnosis: *Varicorbula* of 5–9 mm shell length. Periostracum thick; radial ridges on left valve strong, extending nearly from margin to umbo. Truncation:height ratio (= height of truncated posterior edge of right valve versus total dorsoventral height) 46–52%.

Remarks: *Corbula philippii*, described from Bermuda and Haiti, was included in synonymy with *C. disparilis* [and/or *Varicorbula operculata*] by a number of authors (Dall, 1886; Guppy & Dall, 1896; Lamy, 1941; Aguayo & Jaume, 1950; Pulley, 1953; Anderson, 1996), but is distinct according to the original description and material examined herein. It reaches overall shell lengths equal to those of *V. disparilis*. The radial periostracal ridges on the smaller left valve (Figure 27) are more pronounced than in *V. disparilis* or *V. krebsiana*, and extend nearly up to the umbo. The larger right valve is heavier and more inflated, and has a more pronounced posterior ridge, as well as a more strongly squared posterior truncation.

The truncation:height ratio is greater (46–52%, $n = 6$) than that in either *V. krebsiana* or *V. disparilis*. As in the case of *V. krebsiana*, this species is provisionally maintained as distinct within *Varicorbula* pending further data. It overlaps in distribution (Figure 22) with *V. disparilis* off North Carolina (NCSM/IMS), the eastern and western coasts of Florida (AMNH, ANSP, DMNH, FMNH, HBOM, HMNS; Andrews, 1994) and off Texas (HMNS; Andrews, 1971, 1977, 1981a, b, 1992), and is also recorded from Bermuda (DMNH; Jensen & Harasewych, 1986), Grand Cayman Island (ANSP), the Dominican Republic (AMNH), the Virgin Islands (DMNH), Grenada (ANSP), Tobago (ANSP), and Belize (ANSP). Based on published figures alone (Rios, 1975, 1985, 1994; Vokes & Vokes, 1984), it also occurs in Brazil (Amapá to Rio de Janeiro) and Yucatan. Lamy (1941:219) also mentioned specimens from Martinique which “bien conforme aux figures de Smith.” thus apparently *V. philippii*. Andrews (1981a, b, 1992, 1994; as *C. krebsiana* or *C. operculata*, but figuring *V. philippii*) reported its occurrence off Texas in bamboo-root clumps, commensal with foraminiferans. A similar habit off Texas was earlier noted by Odé & Spears (1970:71; as *Notocorbula operculata*, but identity unverified) as “the attachment root of whip-coral” (see also Odé, 1965) and “in rootmasses washed ashore.” It has been recorded (along with *V. disparilis*, see above) from the gut contents of bottom-feeding starfish (*Astropecten duplicatus*) off North Carolina (Porter & Wolfe, 1971; as *V. operculata*, vouchers NCSM-IMS).

Complete and incomplete boreholes (as described for *Varicorbula disparilis* above) were also noted in specimens of *V. philippii* (AMNH 94733, 248383, 248935, HMNS 7345). One still-articulated specimen of *V. philippii* (HMNS 7345) had five boreholes, three on the larger right valve, and two (including the successful complete one near the umbo) in the smaller left valve.

DISCUSSION

Varicorbula species, either alive or as empty shells, comprise some of the most common bivalved mollusks in benthic samples from the continental shelf of the tropical western Atlantic. Although they were formerly lumped under a single species name, *V. operculata*, this study has recognized the at-least-conchological existence of three separable morphospecies (*V. disparilis* [= *V. limatula*], *V. krebsiana*, *V. philippii*), while ironically relegating the most common species name, *V. operculata*, to the status of *nomen dubium*. Distinguishing shell characters for the three species are summarized in Table 2.

Anatomical data for members of the family Corbulidae are scanty. Those of *Varicorbula gibba*, type of the genus, were described by Yonge (1946); those of *V. disparilis* are described here. The only other genus known anatomically is *Corbula*, exemplified by *C. crassa*, presented by Morton (1990). Uniformity of non-shell char-

Table 2

Distinguishing characters and confirmed distribution of the three western Atlantic species of *Varicorbula*.

	<i>V. disparilis</i>	<i>V. krebsiana</i>	<i>V. philippii</i>
Shell length	5–9 mm	3–5 mm	5–9 mm
Radial ridges on left valve	moderate, margins only	weak	strong, margin to umbo
Periostracum	moderate	moderate	thick
Truncation:height ratio	42–46%	35–39%	46–52%
Distribution (confirmed)	North Carolina, South Carolina, Georgia, Florida, Alabama, Mississippi, Louisiana, Texas, Bahamas, Guadeloupe, Yucatan	Puerto Rico, Jamaica	North Carolina, Florida, Texas, Grand Cayman Island, Dominican Republic, Haiti, Virgin Islands, Martinique, Grenada, Tobago, Belize, Yucatan, Brazil, Bermuda

acters from these three species in two presumed genera lends little support for such characters at the generic level. At the present time, shell characters remain the most important source of characters for defining genera and species within Corbulidae. Because of this paucity of available data, any phylogenetic analysis is premature and is not attempted here.

Varicorbula has been most often placed in the subfamily Corbulinae Gray, 1823 (Keen, 1969; Anderson, 1996) or Caryocorbulinae Vokes, 1945 (Vokes, 1945; Olsson & Harbison, 1953). However, at least two species of *Varicorbula* (the type species, *V. gibba*, and *V. disparilis*; Yonge, 1946, and this study, respectively) have calcification of the marginal siphonal periostracum in the left valve of some specimens. In this respect, *Varicorbula* agrees with the subfamily Caestocorbulinae Vokes, 1945, as originally defined. Although the siphonal calcification in recognized members of this subfamily (e.g., *Caestocorbula* Vincent, 1910, and *Parmicorbula* Vokes, 1944) is more elaborate than in members of *Varicorbula*, the latter agree in all other conchological features with this subfamily and its type genus (shell inequivalve, valves discrepant, left valve less rostrate, left valve with projecting chondrophore, left valve with weaker concentric sculpture and with radial ornamentation, right valve grooved for reception of left valve; Vincent, 1910; Vokes, 1944, 1945). *Notocorbula vicaria* also has been reported with siphonal calcification (Martin, 1918) and may also warrant reclassification to this subfamily. Placement of *Varicorbula* in Caestocorbulinae would extend the paleontologic range of this subfamily from the Cretaceous (Vokes, 1945) to the Recent.

Published accounts of life habits in members of the family Corbulidae (Yonge, 1946: *Varicorbula gibba*; Morton, 1990: *Corbula crassa*; Stanley, 1970: *C. caribaea*) have described very slow-burrowing animals, living close to the surface-sediment interface (reflected by the very short siphons), along with occasional above-surface attachment. Bock & Moore (1968:274) reported that *V. disparilis* (as *Notocorbula operculata*), along with its attached commensal foraminiferan, “climb[ed] above the

flocculent layer close to the bottom” by bysally attaching to *Chaetopterus* worm tubes. The available evidence from these collections, especially the method of capture and apparently random location of attached epifaunal mollusks, agrees with Bock & Moore (1968) by suggesting that *V. disparilis* is more epifaunal/epibyssate than infaunal/endobysate. Whether *V. disparilis* lives a strict epifaunal existence or one among the fragments of coarse “shell hash” is equally undetermined; it is clear that *V. disparilis* in this instance was not buried into finely grained sand or mud. The inequivalve shell and relatively small foot of *V. disparilis* also suggest limited burrowing ability.

Lamprell et al. (1998:366) noted that corbulids often “occur in large numbers in their preferred habitat” (also noted for fossil assemblages by Stenzel et al., 1957) and cited examples of species of *Notocorbula* that are “known to be gregarious.” *Varicorbula gibba* exists in densities up to 600 individuals/m² in the northern Adriatic Sea (Hrs-Brenko, 1981); interestingly, the highest numbers were recorded in polluted harbors. High numbers are also well recorded in the fossil record as corbulid-dominated assemblages (summarized by Lewy & Samtleben, 1979). *Varicorbula disparilis* encountered during this study also existed in large numbers, often as the only living mollusk found in Shipek grab samples, and in a nearly monocultural situation in the dredged byssal mat.

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Simpson (FMNH). Gary Rosenberg (ANSP) shared his unpublished preliminary research on the publication dates of d'Orbigny's contributions to Sagra's *Histoire de l'Île de Cuba*, and also provided access to ANSP collections. Additional access to museum specimens and/or literature was provided by Kathie Way and Joan Pickering (BMNH), Tim Pearce (DMNH), John Wise (HMNS), Daniel Graf (then at MCZ), and Arthur Bogan (NCSM/IMS). Kathie Way (BMNH) and Matthias Glaubrecht (Museum für Naturkunde, Zentralinstitut der Humboldt-Universität zu Berlin) searched their respective Philippi collections for the types of *Corbula operculata*. Two anonymous reviewers provided valuable comments on the manuscript. Bivalve research in our laboratories is supported by U.S. National Science Foundation award DEB-9978119, as part of the Partnerships in Enhancing Expertise in Taxonomy [PEET] Program. This is Smithsonian Marine Station at Fort Pierce Contribution No. 493.

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